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Foot-propelled aquatic birds: pelvic morphology and locomotor performance

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Abstract
The study of ecomorphology (relationship between morphology, ecology and behavior) and biomechanics (relationship between morphology and function) allows identification of ecomorphs and niche inference. It represents an alternative to classical diversity studies, independent from systematic categories, which allows assessment of ecomorphological assemblages in a given ecosystem – a wetland, in this case – based on shape. In this conceptual framework, twenty species of continental aquatic birds from the Pampean region belonging to Anseriformes, Podicipediformes, Charadriiformes and Pelecaniformes were analyzed. Morphology of the pelvic girdle was analyzed by means of geometric morphometrics, assuming that these are foot-propelled birds. Four ecomorphs were identified, comprising, at one extreme, strictly diving form with very dorsally narrow pelves, and at the other, birds with wide pelves and marked angulation between pre- and postacetabular regions, which are good flyers and dabblers but never dive.

Keywords: *Pelvic morphology, geometric morphometric, aquatic birds, thin-plate spline, ecomorphology*

Introduction

Large numbers of marine birds such as penguins, sulids, alcids, and some shearwaters propel themselves under water with their wings. Most commonly in continental aquatic environments, birds use their legs as propellants. This is the style of ducks, grebes, swans and cormorants (Canevari et al. 1991). Locomotion in foot-propelled aquatic birds is strongly associated with hindlimb morphology, and obviously with morphology of the pelvic girdle, with which it functionally coevolves (Johnsgard 1987).

The pelvic girdle provides support for the body mass of the animal, offers anchor points for the hindlimbs and areas for muscle attachment; it is linked with the sacral and caudal regions of the vertebral column. It also offers protection to certain organs, such as the kidneys. Thus, the pelvis has dual functionality; it is involved both in support and protection, on one side, and locomotion and articulation, on the other. In the case of aquatic and subaquatic locomotion, the development and arrangement of pelvic and hindlimb muscles, as well as the extension of muscle attachment surfaces, are particularly important (Johnsgard 1987). There are two distinct regions in the pelvis that are indisputably influenced by muscle attachments and muscle mass, the preacetabular and postacetabular regions. Also, the position and development of the antitrochanter respect to the acetabulum is correlated with hindlimb function (Hertel & Campbell 2007) because this is of particular interest in our study.

The basic assumption underlying all our analyses is that morphology is potentially correlated with the environment and habits of the birds studied, and obviously with their evolutionary history. One of the main goals of the research performed in this work was to establish associations between the different morphological designs and the respective locomotory potentialities. Locomotion, considered here as both speed and direction achieved during movement, is conditioned by the structure of bones and associated muscles. All the birds analyzed here are foot-propelled and, with the exception of grebes and stiff-tailed ducks, they are well adapted for locomotion in air and in water.

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Here we interpret the form-function complex since a nomological perspective in which a phenomenon can be explained from a set of initial conditions and causes that can be tested through deductive methods. Within these types of morphological nomological explanations are located the descriptive morphology and the functional morphology. This is the kind of explanation that we follow in this work.

We use geometric morphometrics to analyze shape of the pelvic girdle of twenty species of aquatic birds that inhabit wetlands in the Pampean Region, Argentina, including ducks, stiff-tail ducks, whistling-ducks, swans, grebes, cormorants and gulls. We establish putative ecomorphs through identification of anatomical features of the pelvic girdle related to swimming-diving habits.

Materials and methods

We studied 83 specimens of foot-propelled birds comprising 11 species of ducks (*Anas*, *Netta*, *Oxyura* and *Dendrocygna*), three species of grebes (*Podiceps* and *Podilymbus*), three species of seagulls (*Larus*), two species of swans (*Coscoroba* and *Cygnus*) and one species of cormorant (*Phalacrocorax*) (Figure 1, Table I). All osseous materials analyzed are housed at Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) in Argentina.

For anatomical nomenclature, we use English equivalents of the terms proposed by Baumel & Witmer (1993) for osteology, and Vanden Berge & Zweers (1993) for myology.

Geometric morphometrics

Each pelvic girdle was photographed in lateral and dorsal view with the same focal length following the guidelines presented by Zelditch et al. (2004), using a Nikon Coolpix 7900 digital camera. Eight homologous points (landmarks) were taken in lateral view and nine in dorsal view (Figure 2; Table II)

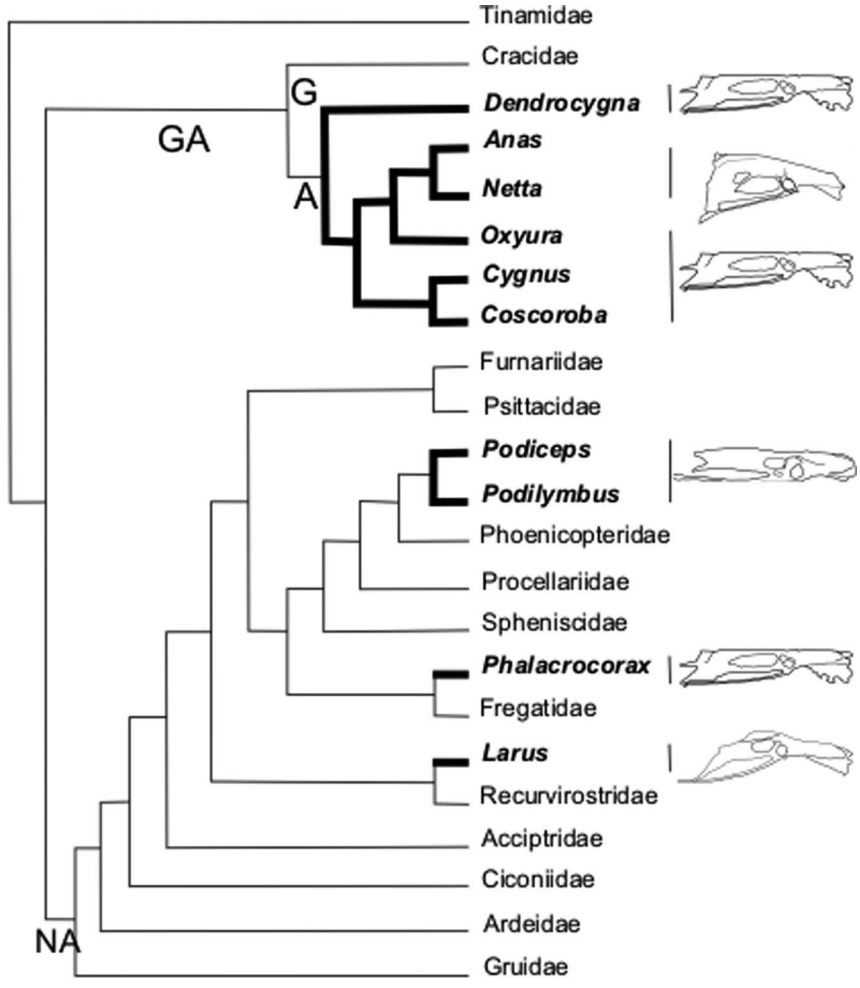

Figure 1. Summary of the relationships of the species used here based on Mayr and Clarke (2003). A, Anseriformes; G, Galliformes; GA, Galloanserae; NA, Neoaves. On the right, pelves in lateral view.

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Table I. List of species examined and individual samples sizes.

Species	N	Abb
Anas cyanoptera	3	Ac
Anas bahamensis	1	Ab
Anas georgica	9	Ag
Anas flavirostris	7	Af
Anas versicolor	6	Av
Anas sibilatrix	13	As
Anas platalea	3	Ap
Dendrocygna bicolor	2	Db
Dendrocygna viduata	2	Dv
Netta peposaca	2	Np
*Oxyura dominica**	1	Od
Cygnus melancoryphus	6	Cm
Coscoroba coscoroba	5	Cc
Podiceps rolland	1	Pr
Podiceps major	8	Pm
Podilymbus podiceps	3	Pp
Phalacrocorax olivaceus	2	Po
Larus dominicanus	7	Ld
Larus cirrocephalus	1	Lc
Larus maculipennis	1	Lm

N. number of specimens; * *(Nomonyx dominicus)*.

Table II. List of landmarks used in the analysis.

N	Definition	Type
	Lateral view	
1	Limit between the isquion and pubis in the acetabulum area	I
2	Dorsal extremity of the antitrochanter	II
3	Pectineal process	II
4	Anterior extremity of the ilion	III
5	Anterior point of the median dorsal ridge	III
6	Dorsal border at level of pectineal process	II
7	Posterior extremity of the isquion	III
8	Ventroposterior extremity of the isquion	III
	Dorsal view	
1	Anterior point of the median dorsal ridge	III
2	Anterior extremity of the ilion	III
3	Pectineal process	II
4	Antitrochanter	II
5	Mid point of the median dorsal ridge	II
6	Mid point of dorsal isquion	II
7	Mid point of ventral isquin	II
8	Posterior point of the median dorsal ridge	III
9	Ventroposterior extremity of the isquion	III

N. number of landmarks in Figure 2A, B. Types I, II and III following Monteiro (1999).

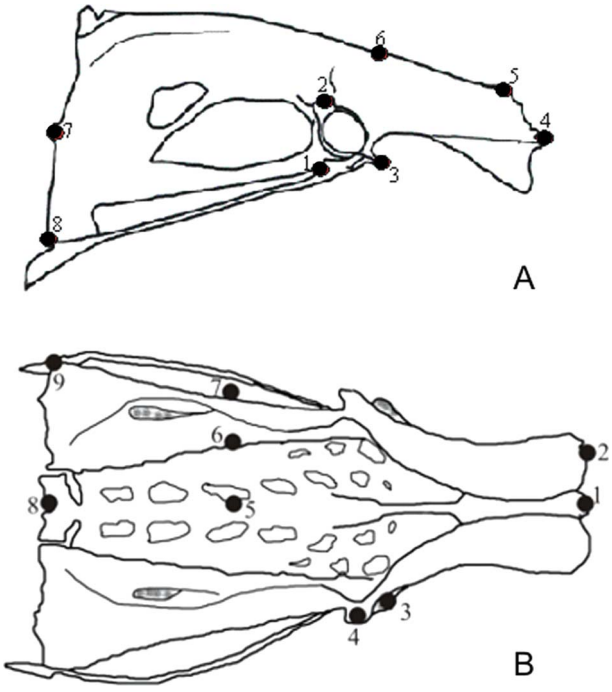

Figure 2. Landmarks used in the analysis in (A) dorsal view, (B) lateral view. For definition of landmarks see Table II.

for each specimen. Landmarks used were type I, II and III (Monteiro 1999; Monteiro & Abe 1999). Photographs were calibrated and the *x* and *y* coordinates of each landmark were digitized using TPSDig 2.04 software (Rohlf 2004).

The effect of location, size and orientation ("non shape variation") were removed of the resulting coordinates by General Procrustes Analysis (GPA, Rohlf & Slice 1990; Zelditch et al. 2004). Then we analyzed shape changes using thin plate splines (Bookstein 1991; Zelditch et al. 2004). Once the consensus configuration for each species was obtained a Relative Warps Analysis (RWA, a principal component analysis of the partial warp scores; Rohlf 1993) was performed to examine pelvic shape changes. The RWA was made using TPSRelw 1.41 software (Rohlf 2004). A value of zero for the alpha parameter was used for this analysis, as recommended for taxonomical and exploratory studies (Rohlf 1993), to emphasize differences at both large and small scale. To evaluate differences in the pelvic shape between the groups resultant of the RWA, a MANOVA was performed using ecomorph (diving; diving-volant; volant and dabbling birds) as independent variable and the partial warp and uniform component scores as dependent variables. Locomotor performance was taken from Canevari et al. (1991).

Results

Relative Warps Analysis in dorsal view showed four groups (Figure 3): one formed by *Podiceps major, Podiceps rolland* and *Podilymbus podiceps*; the second formed by *Cygnus melancoryphus, Coscoroba coscoroba, Dendrocygna viduata, Dendrocygna bicolor, Phalacrocorax olivaceus, Netta peposaca* and *Oxyura dominica*. The third group comprised *Anas platalea,*

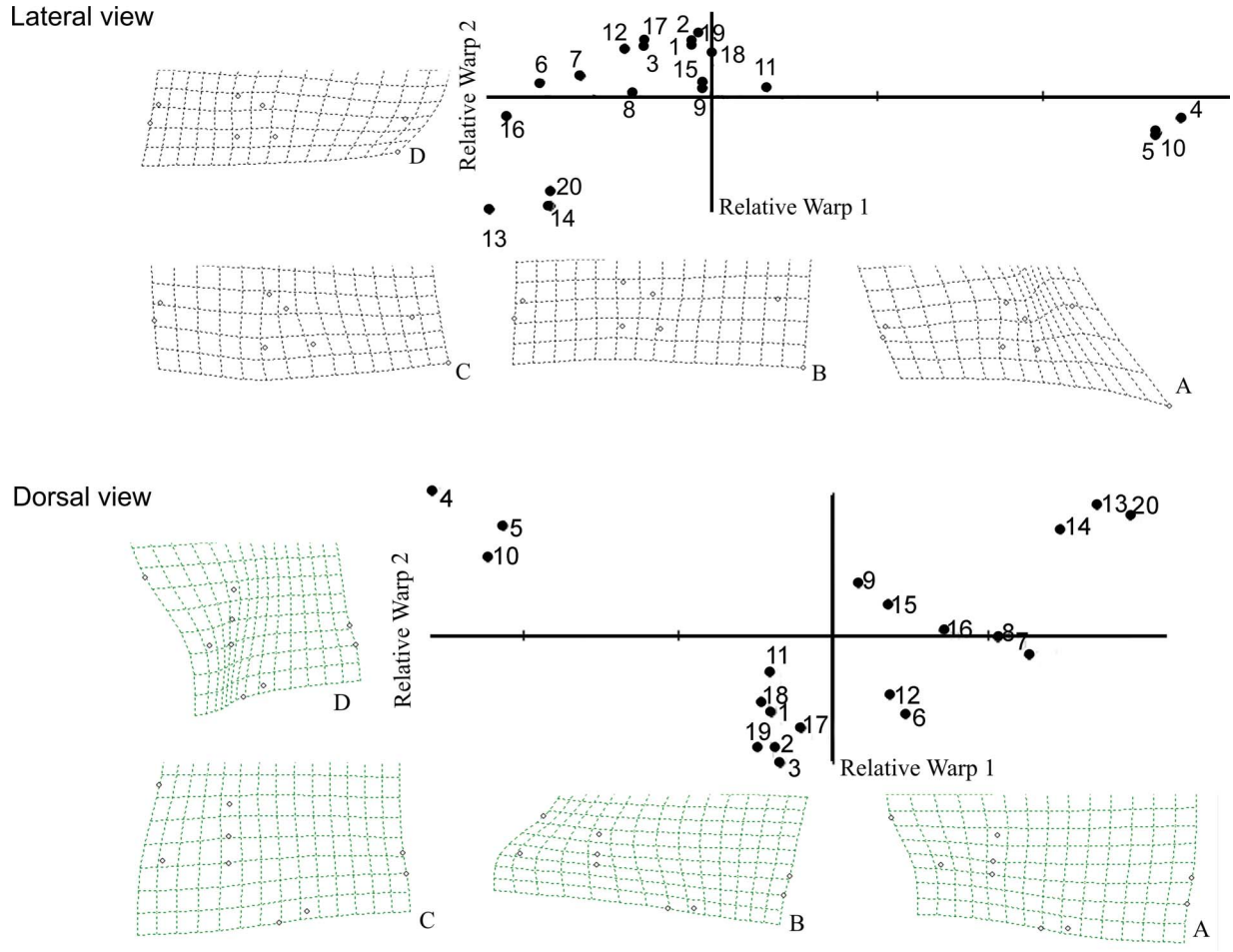

Figure 3. Relative warp (RW) for values $\alpha = 0$ of pelves in lateral and dorsal view. Grids show the visualization of shape changes in each species. **A**) variation in the shape of the pelves as positive deviations of the mean in the axis of relative warps 1; **B**) variation in the shape of the pelves as positive deviations of the mean in the axis of the relative warps 2; **C**) variation in the shape of the pelves as negative deviations of the mean in the axis of relative warps 1; **D**) variation in the shape of the of the pelves as negative deviations of the mean in the axis of relative warps 2. 1- *A. versicolor*, 2- *A. flavirostris*, 3- *A. sibilatrix*, 4- *L. cirrocephalus*, 5- *L. maculipennis*, 6- *O. dominica*, 7- *C. melancoryphus*, 8- *C. coscoroba*, 9- *D. viduata*, 10- *L. dominicanus*, 11- *A. bahamensis*, 12- *N. peposaca*, 13- *P. major*, 14- *P. rolland*, 15- *D. bicolor*, 16- *P. olivaceus*, 17- *A. georgica*, 18- *A. cyanoptera*, 19- *A. platalea*, 20- *P. podiceps*. Black dots represent the consensus configuration for each species.

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Anas cyanoptera, Anas sibilatrix, Anas bahamensis, Anas georgica, Anas flavirostris, and *Anas versicolor*; and finally, a fourth group clustered the larids – *Larus maculipennis, Larus cirrocephalus* and *Larus dominicanus*-. Despite Relative Warp Analysis in lateral view confirmed a clear separation between the ecomophs one and four did not show a clear separation between the ecomorphs two and three.

The axis of greatest variation (first relative warp) explained 85% in lateral view and 75% in dorsal view of the total shape variation. The second relative warp explained 6% in lateral view and 16% in dorsal view of all the observed variation.

In terms of shape of the pelvic girdle, the main morphological differences among the four groups are associated with the postacetabular zone in lateral and dorsal view. Several morphological differences in lateral view can be pointed out. In larids (Figure 3) the dorsal region of the postacetabular pelvic region is narrowed (landmarks 6, 7), whereas the caudoventral region is expanded (landmarks 7, 8). On the contrary, the pelvic girdle of grebes is expanded dorsally and narrowed caudally. The other two groups are morphologically intermediate. There is also an important difference in the height of the acetabular zone (landmarks 3, 6), which is minimal in larids and maximal in grebes.

A noteworthy difference between the pelvic girdles compared is the angle between the pre- and postacetabular regions. In lateral view, grebes show a markedly straight dorsal margin (landmarks 5, 6, 7), whereas larids show evident angulation.

In dorsal view, it is evident that the postacetabular region is much shorter (landmarks 5, 8) in the fourth group – larids-. The opposite is verified in the grebes, with marked posterior elongation (landmarks 5, 8) and mediolateral narrowing, so that the dorsal margins of the ischia are very close to each other (landmarks 5, 6).

The results of MANOVA indicate that the shape differences of the pelvic girdle in lateral and dorsal view were highly significant between groups founded in the RWA, both for uniform and non-uniform components (Lateral view: Wilks'λ 0.015, $P < 0.001$; dorsal view: Wilks'λ 0.0282, $P < 0.0001$).

Discussion

In this study, we examined variation in pelvic girdle shape and locomotor performance in several aquatic continental birds from the Pampean region. Geometric morphometric indicated the existence of well-marked differences related to pelvic shape in the species analyzed and showed differences in both dorsal and lateral views, primarily at the postacetabular region. Similar ecomorphological assemblages -diving birds, volant birds, diving-volant and dabbling birds- were obtained from classical statistical analyses of hindlimb bones (Ibáñez 2006).

Despite the fact that morphology of the birds studied is potentially correlated with their evolutionary history, here we have avoided applying phylogenetic comparative methods to evaluate whether the similarities found in the pelvis shape are due to phylogenetic constrain or have adaptive nature. Unfortunately, we have not detailed ancestor–descendant relationships in the context of a reasonably sized phylogeny and reliable trait information for ancestors for the species used here. Symonds (2002: 552) says in this sense: "Using a phylogeny may not be so important in an analysis at higher taxonomic levels because the groups involved are more distant from their common ancestor and will have experienced considerably more independent evolution". The sample of species studied here seems to be the case.

We mentioned previously that there are two distinct regions in the pelvis that are indisputably influenced by muscle attachments and muscle mass. One of them is the preacetabular region, which offers surface areas for the insertion of the protractor and flexor muscles of the femur (Figure 4). *M. iliotibialis cranialis* originates from the craneodorsal margin of the preacetabular iliac crest and inserts on the medial surface of the patella (rotulian ligament) or the proximal region of the tibiotarsus (Raikow 1985). *M. iliotibialis lateralis* originates from the iliac crest

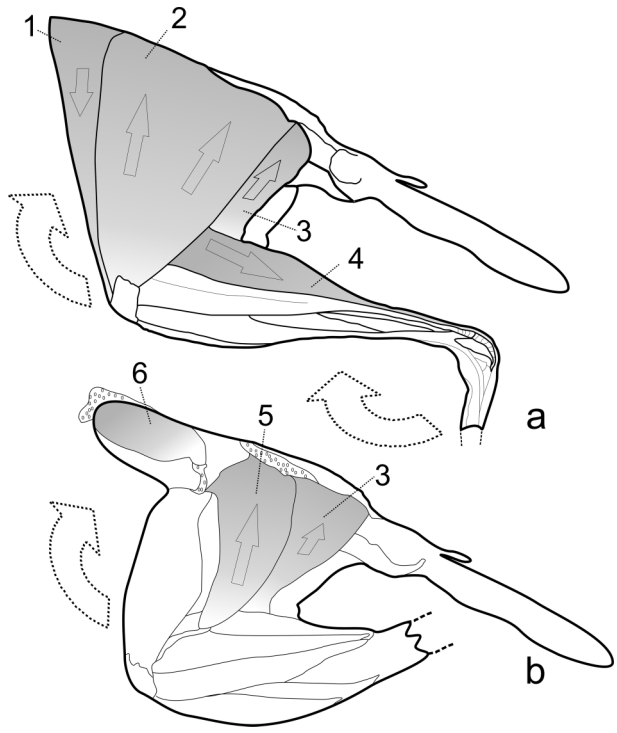

Figure 4. Schematics illustrations of the main muscles of the hip joint and leg of a coot in left lateral view; (a) superficial muscles, (b) deep muscles. 1 m. iliotibialis cranialis (acts as a flexor of the hip); 2 m. iliotibialis lateralis (acts as extensor of the hip joint); 3 m. flexor cruris pars lateralis (acts as extensor of the hip joint); 4 m. gastrocnemius pars lateralis (its contraction extend the ankle); 5 m. iliofibularis (acts as a flexor of the knee); 6 m. iliotrochantericus caudalis (its contraction extend the hip). Arrows indicate the main lines of action of the muscles.

and inserts on the proxima surface of the tibiotarsus. Lastly, *m. iliotronchantericus caudalis* originates from the lateral surface of the preacetabular ilion and inserts on the trochanteric crest on the lateral surface of the femur. Two major knee-joint flexor muscles originate from the postacetabular pelvic area: *m. iliofibularis*, which inserts on the proximal end of the fibula, between the external and medial heads of *m. gastrocnemius*, and *m. flexor cruris lateralis*, which inserts on the medial surface of the proximal tibiotarsus (Figure 4; Rosser et al. 1982).

Phalacrocorax has a more developed postacetabular region with respect to the preacetabular region, and well-marked *crista dorlateralis ilii*. This suggests good development of femoral extensor muscles and consequently, extensive femur movement.

More restricted femur movement and strong knee-joint flexion occur in *Podiceps* and *Podilymbus*, as evidenced by greater relative length of the postacetabular region and greater development of respective flexors. This combines with the subparallel position of the femur with respect to the proximo-distal axis

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of the pelvic girdle (Johnsgard 1987; Ibáñez 2006). Although these interpretations of the pelvic-muscle relationship are ultimately an oversimplification of a highly complex system, give a basic idea of the morphological and functional implications of the differential development of the pelvis and associated muscles in the four different ecomorphs.

Landmarks 2 and 5 described the spatial position of the antitrochanter with regard to the dorsal area of the pelvis. Pelves with landmarks 2 and 5 widely separated have high dorso-ventral development at the acetabulum level. *Podiceps rolland, Podilymbus podiceps* and *Podiceps major* have this type of pelveses. Coincidentally the presence of high antitrochanteric angles (in lateral view, the angle between the long axis of the antitrochanter in relation to the vertebral column, Hertel & Campbell 2006) also occurs in grebes. The position and development of the antitrochanter in combination with the femur morphology, allows their legs to position farther posterior, in line with the long axis of the body, an optimal design to underwater movement. Comparatively, dabbling ducks and gulls have wider pelves and the least relative height at the acetabular area in the opposite direction as grebes.

On the basis of the methods applied, four morphs were identified mainly differentiated by the morphology of the postacetabular zone. These comprise, in one end of the variation range, pelvic girdles characterized by little separation between the dorsal margins of the ischia, greater height at the acetabular zone, and pre- and postacetabular regions unequally developed and forming a 180° angle to each other. At the other extreme, a second morph comprises girdles with large dorsal separation between the ischia, lesser height at the acetabular zone, greater development of the preacetabular region, and marked angulation between pre- and postacetabular regions. The third morph comprises forms with intermediate separation between the dorsal margins of ischia, scarce separation between antitrochanters, and large height at the acetabular zone; finally, a fourth morph includes pelves with ischia more separated than in the previous morph, large separation between antitrochanters, and little height at the acetabular zone.

The morphology of the pelvic girdle of grebes (*Podiceps major, Podiceps rolland* and *Podilymbus podiceps*) corresponds to the first morph described. These birds are typical divers, with reduced bone pneumaticity (Johnsgard 1987; Llimona & del Hoyo 1992); their hindlimbs are situated posteriorly (Hertel & Campbell 2006), providing a more hydrodynamic profile that is nevertheless adequate for land locomotion; on the contrary, their wings are extremely short with poorly developed muscles (Johnsgard 1987). Direct observations by one of the authors (Ibáñez 2006) in wetlands of the Pampean Region have shown that these birds generally are found in open waters with no aquatic vegetation, at the central areas of water bodies. If threatened, they dive and move long distances underwater without flying; the latter requires them to perform prolonged paddling across the water surface, during which they actively move their wings and hindlimbs.

Gull species, *Larus dominicanus, Larus maculipennis* and *Larus cirrocephalus* are included in the second morph. These birds are well-known skilled flyers (Lewington 1992), with great ability to glide and travel long distances on a daily basis. Observations of these birds in their natural environments show that in order to catch their prey, they dive from the air and may plunge into the water, but never dive (Canevari et al. 1991). They do not usually use their legs for locomotion in water; rather, they rest on the surface and drift with the currents. They are generally found in open waters or at rest on the shore, but never among emergent plants. In spite of their webbed feet, they move deftly on land.

The third morph is represented by the species *Phalacrocorax olivaceus, Oxyura dominica, Dendrocygna viduata* and *Dendrocygna bicolor.* This group comprises birds that dive during the day - *Phalacrocorax olivaceus* and *Oxyura dominica* - as well as others that dive at night - *Dendrocygna viduata* and *Dendrocygna bicolor*. All of them have good flying ability, but require prolonged paddling across the water surface to take off (Canevari et al. 1991; Carboneras 1992). Both *Phalacrocorax olivaceus* and *Oxyura dominica* walk awkwardly on land, due to the very posterior position of their hindlimbs. They swim dexterously, with their body almost completely submerged and only the head and neck rising above the water level (Carboneras 1992; Orta 1992). On the contrary, *Dendrocygna viduata* and *Dendrocygna bicolor* stay near lagoon shores forming congregations of hundreds of individuals during most of the day, and are mostly active at night. Remarkably, the swans *Coscoroba* and *Cygnus* were clustered with this ecomorph. We are not able to find any ecological explanation for this.

The fourth ecomorph is represented by the species *Anas platalea, Anas flavirostris, Anas cyanoptera, Anas georgica, Anas sibilatrix, Anas versicolor, Anas bahamensis* and *Netta peposaca*. All these birds are typical dabblers, not divers; they usually fly and walk well (Carboneras 1992). In order to feed, they may skim the water surface using the beak, submerge the head, upend half of the body, or graze, depending on the species, the type of food and their location.

They spend most of the daytime feeding in the water (Canevari et al. 1991).

A larger sample size is necessary before building solidly based functional interpretations, but our data show four pelves shapes associated to dissimilar modes of locomotion and from distantly related families. Theoretically, species that occupy homogeneous habitats may show niche partition, and this could be expressed in both their behavior and their pelvic morphology. This is precisely what was verified in the case of the birds studied here, which occupy the same wetland and exploit resources differentially, in terms of diurnal-nocturnal activity, preferred water depth and vegetation abundance.

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